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EFFECTS OF WATER TABLE DEPTH AND EDAPHIC CHARACTERISTICS ON
PLANT DIVERSITY IN A SOUTHERN MISSISSIPPI PITCHER PLANT BOG

by

Patrick M. Kirby

A Thesis

Submitted to the Graduate School,
the College of Arts and Sciences
and the School of Biological, Environmental, and Earth Sciences
at The University of Southern Mississippi
in Partial Fulfillment of the Requirements
for the Degree of Master of Science

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ABSTRACT

This study examined the effects that water table depth and soil characteristics have on plant species richness and species composition within pitcher plant bogs across seasons. Eight piezometers were installed at random distances to monitor long-term water table depth and pressure fluctuations along a ~710-meter line transect traversing upland and bog habitats. Vegetation sampling quadrats (n=128) were set up near each piezometer. Cover data and water table depths were collected in spring and late summer. Soil samples collected from each treatment group were used to obtain soil texture and nutrient data. The summer collection period yielded a total γ diversity of 152 taxa, while the spring resulted in a γ diversity of 149 taxa. Grasses, sedges, and forbs were the most abundant species across both sampling seasons. Regression indicated that mean species richness was not significantly dependent on mean water table depth [$P=0.1313$]. Regression also concluded that mean percentage of sand in the soil had a significant, positive effect on mean water table depth [$P=0.003$]. It was proposed that soil moisture levels are contributing to levels of diversity due to the mesic treatments exhibiting the highest levels of plant diversity across both sampling seasons. Statistical analyses provided evidence that soil moisture and soil texture could be gradients driving plant species composition.

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DEDICATION

This thesis would not have been possible without the support of my family, friends, colleagues, and advisors. I thank my parents for instilling a sense of passion for nature and conservationism. I hope to make my university and professors proud throughout my career in environmental biology.

TABLE OF CONTENTS

| | |
|---|------|
| ABSTRACT | ii |
| ACKNOWLEDGMENTS | iii |
| DEDICATION | iv |
| LIST OF TABLES | vii |
| LIST OF ILLUSTRATIONS | viii |
| LIST OF ABBREVIATIONS | ix |
| CHAPTER I - INTRODUCTION | 1 |
| CHAPTER II – METHODS | 7 |
| Study Site | 7 |
| Study Plots | 7 |
| Water Table Depth | 8 |
| Vegetation Sampling | 8 |
| Soil Data | 9 |
| Soil Nutrient Analyses | 9 |
| Weather Station Data | 10 |
| Multivariate Statistical Analyses | 10 |
| Diversity, Abundance, ANOSIM and NMDS | 10 |
| Univariate Statistical Analyses | 11 |
| Parametric Assumptions | 11 |

| | |
|---|----|
| Analyses of Variance (ANOVA) and Kruskal-Wallis Tests | 11 |
| Factorial Analysis of Variance..... | 12 |
| Simple Linear Regressions | 12 |
| CHAPTER III - RESULTS..... | 13 |
| Richness, Abundance, and Community Similarity | 13 |
| Parametric Normality | 14 |
| Effect of Seasonality and Piezometer Location | 15 |
| Species Richness Differences per Season..... | 15 |
| Water Table Depth Differences per Season..... | 15 |
| Soil Texture Differences | 16 |
| Soil Carbon | 16 |
| Soil Nitrogen..... | 17 |
| Soil Phosphorus | 17 |
| Dependency of Environmental Factors..... | 17 |
| CHAPTER IV – DISCUSSION..... | 18 |
| APPENDIX– Tables and Figures | 23 |
| REFERENCES | 37 |

LIST OF TABLES

| | |
|--|----|
| Table A1. August 2018 Top 25 Species (Percent Cover) | 23 |
| Table A2. April 2019 Top 25 Species (Percent Cover) | 25 |
| Table A3. Wet Treatment Group's Top 10 Species (Percent Cover) | 27 |
| Table A4. Dry Treatment Group's Top 10 Species (Percent Cover)..... | 28 |

LIST OF ILLUSTRATIONS

| | |
|---|----|
| Figure A1. Species Accumulation Curves | 29 |
| Figure A2. Analyses of Similarity | 30 |
| Figure A3. NMDS Ordinations for Summer 2018 and Spring 2019 | 31 |
| Figure A4. Two Factor, Factorial ANOVA Interaction Plot | 32 |
| Figure A5. Mean Species Richness for Each Treatment Group | 33 |
| Figure A6. Mean Water Table Depth for Each Treatment Group | 34 |
| Figure A7. Mean Percent Sand in the Soil for Each Treatment Group | 35 |
| Figure A8. Simple Linear Regressions of Edaphic Characteristics | 36 |

LIST OF ABBREVIATIONS

| | |
|---------------|---|
| <i>USM</i> | The University of Southern Mississippi |
| <i>GCP</i> | Gulf Coastal Plain |
| <i>DNF</i> | DeSoto National Forest |
| <i>USDA</i> | United States Department of Agriculture |
| <i>NRCS</i> | Natural Resources Conservation Service |
| <i>ANOSIM</i> | Analysis of Similarity |
| <i>NMDS</i> | Non-metric Multidimensional Scaling |
| <i>ANOVA</i> | Analysis of Variance |

CHAPTER I - INTRODUCTION

In the Gulf Coastal Plain (GCP) of the southeastern United States, boggy grasslands form from sloping, underground seepages of ground water coupled with ample annual precipitation. Bog formation in this region relies primarily on soil texture, composition, and parent material (Folkerts 1991). The upper soil horizons are largely composed of sand and silt loams that often abruptly transition to lower clay-rich horizons (Folkerts 1982). These clay horizons are naturally impermeable to percolating groundwater and can result in the persistence of extensive underground water tables (Enge 2002). In these soils, percolating water is forced to disperse laterally forming expansive wetland habitats known as seepage bogs (Folkerts 1991). These bogs are often deficient in one or more plant nutrients resulting in the evolution of carnivory in several plant genera.

Pitcher plant bogs in the GCP are often nested within larger tracts of longleaf pine forests. The loss of longleaf pine forests (> 60% post European colonization) has resulted in a similar loss of pitcher plant bogs within the GCP. Up to 97% of GCP pitcher plant bogs had disappeared by the early 1980s (Folkerts 1982). Despite large-scale habitat loss and fragmentation these bogs still occur across longleaf pine-dominated ecosystems of the Southeast and can be found throughout the DeSoto District of the DeSoto National Forest (DNF) in South Mississippi. Buttercup Flats is one of these sites and is one of largest, continuous pitcher plant bogs in the world.

Buttercup Flats is in Stone County, Mississippi, in DNF. According to the USDA's Natural Resources Conservation Service (NRCS), bog soils in DNF derive from clayey marine deposits and exhibit slow hydraulic conductivity rates (ksat) (Soil Survey

Staff 2017). The NRCS has classified the soil profile of Buttercup Flats and determined the primary soil type of its compartment as Susquehanna silt loam. Susquehanna silt loam constitutes nearly 75% of the soil profile at Buttercup Flats. Susquehanna silt loam exhibits an undulating characteristic of two prominent soil horizons; the first (top layer) horizon is composed of fine sandy/silt loams ranging 0–8 inches in depth, while the second horizon is composed of a dense clay layer ranging from 8-61 inches in depth. Generally, silt loams are relatively porous and fine textured; therefore, they exhibit lower bulk densities and hydraulic conductivity rates than coarser soils (Rawls and Brakensiek 1983; Rawls et al 1993). Clay-dominant soils are the finest textured soil components and typically have the lowest bulk densities, but they are quite compactable, which increases the overall bulk density and decreases porosity as depth of the soil profile increases (Rawls 1983; Rawls et al 1993). Clark et al. (2008) observed the soil moisture at Buttercup Flats for fourteen days over two months, measuring the lowest in September and the highest in wintering months. Slow infiltration of water combined with ample precipitation provides the boggy conditions needed for numerous plant species to establish and thrive within wet savanna ecosystems.

Longleaf pine savannah bogs have high levels of biodiversity that are typical of warm, humid, subtropical habitats (Mittelbach et al. 2007). The climate of the Gulf Coastal Plain States is characteristically subtropical exhibiting hot, humid temperatures with seasonal patterns of precipitation, and high seasonal effects on evapotranspiration rates (Mulholland et al. 1998). My study site receives a mean precipitation of 60-75 inches and mean air temperature of 64-70 °F (NRCS). Bogs in this region are largely

patchy, but patches often harbor diverse plant assemblages composed of both herbaceous and woody species.

George W. Folkerts (1982) estimated that longleaf pine savanna bogs along the Gulf Coast, such as Buttercup Flats, possess some of the most diverse carnivorous plant assemblages in North America and possibly the world. The carnivorous flora of pine savanna bogs comprise species from several genera, including the sundews (*Drosera*), bladderworts (*Utricularia*), butterworts (*Pinguicula*) and pitcher plants (*Sarracenia*) (Folkerts 1982). Prevalence of carnivorous plants is indicative of wet habitats because carnivory is a more advantageous trait in moist, nutrient deficient environments (Brewer et al. 2011). Species from the pitcher plant family, *Sarraceniaceae*, are some of the most abundant carnivorous plants in pine savanna bogs. The pale pitcher plant, *Sarracenia alata*, is a common species found in the Gulf Coastal plain and serves as the namesake for Buttercup Flats (Mize et al. 2005). While carnivorous plants are important members of bog plant assemblages, a multitude of non-carnivorous, herbaceous and woody species inhabit savanna bogs.

Clark et al. (2008) studied frequencies of dominant plant species occurring within longleaf pine (*Pinus palustris*) savannas in southern Mississippi and Louisiana; Buttercup Flats served as one of their study sites. They concluded that the majority of the dominant species in terms of species frequency belonged to several genera from the Order *Poales*. The most dominant included the grass genera *Schizachyrium*, *Andropogon*, *Aristida*, and *Dichanthelium*, as well as sedge genera *Rhynchospora* and *Scleria* (Clark et al. 2008). Woody plant diversity is normally much lower than herbaceous diversity within well-managed savanna habitat. Clark et al. (2008) calculated infrequent distributions, meaning

most species in the sampling group occurred in only 10% of the study sites. They concluded that Buttercup Flats and other pine savanna bogs alike may be lacking the presence of core or satellite species; they hypothesized that the resulting unimodal species distributions could be attributed to heterogeneity of environmental factors across the sampled longleaf pine savannas. It was postulated that environmental factor variability, such as fluctuating soil moisture, nutrient availability, and disturbance, create microhabitats where only certain species can specialize.

Historically, longleaf pine ecosystems stretched across the southeastern United States for millions of hectares (Noss 1989). Extant longleaf habitat still exists but has been dramatically reduced via anthropogenic activities, such as timber operations (e.g., turpentine and logging) and habitat conversion/destruction (Gilliam and Platt 1997; Frost 1993). Like most longleaf pine ecosystems, savanna bog ecosystems need fire in order for plant assemblages to thrive. Frequent, low intensity disturbance via fire is a critical component to conserving these ecosystems and has been vital in the natural history of the southeastern U.S. (Glitzenstein et al. 1995). Suppression of fire results in successional habitat loss via tree/shrub invasion (Tucker and Robinson 2003). The longer fire is absent from a system the more depauperate the understory becomes, with hardwood trees and large shrubs replacing diverse assemblages of grasses, forbs, and subshrubs (Glitzenstein et al. 2003). This dependency on fire has resulted in plant species becoming both fire tolerant and dependent (Gilliam and Platt, 1997; Mutch 1970). Hence, fire suppression often results in low plant diversity.

Longleaf pine communities in South Mississippi are subjected to some of the most aggressive management regimes in the country. The U.S. Forest Service primarily

manages DNF for timber production, restoration, and recreation (Kupfer et al. 2008). Forest thinning and prescribed burning are both heavily relied upon management techniques for restoring pine forest diversity. Buttercup Flats has been subjected to management via thinning in the past and is regularly burned on a 1–3-year cycle (Sykes et al. 1994). Consistent management of Buttercup Flats has largely restored the diversity of this wetland savanna and is a good reference for the benefits of proper forest management and for future ecological restoration activities. Wet pine savannas are largely understudied because many of these habitats are fragmented or degraded due to habitat loss and mismanagement. Studying sites like Buttercup Flats is vital in understanding key ecological processes shaping native plant assemblages along the Gulf Coast Plain.

Soil texture derives its characteristics largely on the decomposition of unique parent materials and deposition via climatic events over time; therefore, texture may serve as a crucial determinant of longleaf savannah community structure (Solbrig 1996; Drewa et al. 2002)

Past studies of savanna/bog habitats have primarily focused on species composition and frequency, restoration/remediation techniques, entomological/zoological research, and species-specific plant interactions. Very few studies have examined the effect of specific abiotic factors on wet, pine savanna ecosystems. The impact that environmental factors, such as soil moisture, soil texture, and seasonality, have on diverse plant assemblages within wetland pine savannas needs to be further investigated. Therefore, the aim of this study is to determine any significant effects that seasonality,

water table depth, and soil texture, have on plant species richness within wet, longleaf pine savannas.

In this study, three objectives were addressed regarding environmental factors driving plant community structure and species richness in longleaf pine savannah bogs.

1. Characterize dominant species that occur along the water table depth gradient and compare similarity in species compositions among varying locations along the water table gradient.
2. Determine if there is an interaction of seasonality and water table depth affecting species richness.
3. Determine if differences in soil texture interact with species richness and water table depth.

CHAPTER II – METHODS

Study Site

Buttercup Flats in De Soto National Forest served as the study site for this project. Buttercup Flats is an extensive network of pitcher plant bogs interspersed with raised ‘islands’ of pine savannahs. The bogs at Buttercup Flats have been used in previous studies that examined spatial diversity patterns (Clark et al. 2008; Seigrist 2006) and convergence pitcher fluid communities (Bittleston 2016). The soils in the bog areas are primarily undulating Suquehanna silt loam while the islands are undulating Saucier fine sandy loam or undulating Benndale fine sandy loam (USDA Web Soil Survey). Pitcher plant bogs in the GCP do not resemble *Sphagnum* (peat moss) bogs from more northern latitudes (Folkerts 1982). Unlike northern bogs, these bogs do not retain large amounts of surface water, rarely flood, and have low hydrologic energy (Folkerts 1982). Most bogs within the Buttercup Flats network are not hillside seepage bogs (sensu Folkerts 1982), however, small topographical gradients exist across the landscape.

Study Plots

Eight piezometers were installed along a 710 m line transect to monitor long-term water table depth and pressure fluctuations. Piezometers were installed at random distances from each other in order to sample as much topographic variability as possible along the transect. Around each piezometer, four plots were systematically established using a compass to divide the area around each plot into four directional quadrants. Four sampling quadrats (2x2 m) were established within each quadrant at a random distance from the center (2-15 m) and at a random compass bearing. This yielded 16 quadrats around each piezometer for a total of 128 quadrats along the entire transect.

Water Table Depth

Water table depth data were collected using eight previously installed piezometers. The piezometer locations occur at random distances across ~600 m elevational gradient at Buttercup Flats. The piezometers were constructed out of 2.5 diameter PVC pipe. As in Floyd (2010), slits were carved on the bottom section of the PVC (~40 cm) to facilitate the movement of subsurface water. Holes for each piezometer were bored ~1.0-meter-deep depending on the location along the elevational gradient and ~0.69 meters wide (Floyd 2010). The PVC pipe was placed and centered in the hole, backfilled with gravel within 15 cm of the soil surface, and then the remaining space was filled with bentonite (Floyd 2010). The bentonite was used to seal the top and prevent surface infiltration during flooding from heavy precipitation events.

Onset HOBO Data Loggers (Onset Computer Corporation, Bourne, MA, U.S.A.) were used to record water table depth, pressure, and temperature data every 12 hours in the piezometers. Data were downloaded in the field using the HOBOWare software, laptop, and Optic USB interface. Mean water table depth for each piezometer was calculated by averaging 60 days of recorded depths. The depth averages were calculated for 60 days prior to each seasonal herbaceous cover collection.

Vegetation Sampling

Percent cover of all species were recorded within each quadrat in August 2018 and April 2019. All vegetation data collection for each date were completed within four days. Species richness was calculated for each quadrat.

Soil Data

Soil cores were collected at each the four plots around each piezometer (32 total cores). Cores were collected using a 1-1/8" diameter slotted soil probe with 1" × 12" butyrate core sleeves (AMS, Inc., American Falls, ID). Soil cores were kept frozen until processed.

Soil texture was estimated by sieving dried samples. Samples were dried in a forced air-drying oven for three days at 70°C. The samples were then individually homogenized to remove peds by gently grinding with a mortar and pestle. The homogenized soil was then sieved through a 250-micron sieve to further disperse soil separates. All material retained on the sieve was again crushed using a mortar and pestle. The entire sample was then sieved through a 125-micron sieve. Once again, all retained material would be broken down via mortar and pestle. This process of using the 125-micron sieve was repeated until a consistent retention of material was yielded. The retained material was then weighed, so that percent composition of sand could be determined using the weight of the entire soil sample. Gee and Or (2002) state the typical particle-size range of separated sand from the soil is 50-2000 microns; therefore, it was determined that 125-micron sieve would give an adequate estimate of percent sand in each soil sample. Though, Day (1965) posited there is a high probability that some sand particles are passed through the sieve due to variability in the size, nature, and properties of sandy separates (Gee and Or 2002).

Soil Nutrient Analyses

The homogenized fine particulate matter leftover from the texture analysis was then prepared for nutrient analyses. An ECS 4010 Nitrogen/Protein Analyzer was used to test for carbon and nitrogen concentration in the soil, but first 20 mg of each soil sample

had to be encapsulated in aluminum foil. Each sample was weighed separately, then delicately enclosed in the foil into a compact sphere. Phosphorus concentrations of corresponding subsamples of soil from the above analysis were determined using the methods adhered to by Su et al. (2015). For this phosphorus analysis, soil subsamples were weighed (~300 mg) into 20 x 125 mm glass vials. The vials were then placed in a muffle oven and combusted at 500°C for at least 3 hours. The ash that remained after combustion was solubilized in 1N HCl acid then diluted with distilled water. Phosphorus concentrations were determined using a SEAL AA3 Flow Injection Nutrient Analyzer (molybdate-ascorbic acid method).

Weather Station Data

Weather data were obtained from the U.S. Forest Service's Remote Automatic Weather Station (RAWS) at Black Creek. Data were accessed via the Western Regional Climate Center's website. Estimated evapotranspiration rates were calculated using the Penman-Monteith Method.

Multivariate Statistical Analyses

Diversity, Abundance, ANOSIM and NMDS

Using RStudio statistical software, species richness, abundance, composition and similarity were calculated. Similarities in species composition at each treatment group over each season were examined using an analysis of similarity (ANOSIM) of Bray-Curtis similarity coupled with a non-metric multidimensional scaling (NMDS) ordination. ANOSIM's rank dissimilarities in the sampling groups, allowing for the comparison of between and among rank similarities of the treatment groups.

NMDS is a visualization of the sample's rank similarity differences in dimensional space. Analyses of similarity tests were also utilized to compare functional group richness for each treatment group.

Univariate Statistical Analyses

Parametric Assumptions

After sampling species percent cover and water table depth from each of the eight piezometer populations over summer and spring seasons, specific statistical tests were determined to be appropriate analyses for this study. All univariate statistical analyses were computed in JMP statistical software (company info) using an alpha of 0.05. Before running the analyses, the parametric test assumptions were verified. Eight Shapiro-Wilk goodness of fit tests were run to verify each of the populations at the eight piezometers are normally distributed in terms of mean water table depths, mean percent sand in the soil, and mean species richness. Next, eight Bartlett's tests were required to test the null hypothesis that the variances of all the populations of piezometers are equal in terms of mean water table depths, mean percent sand in the soil, and mean species richness.

Analyses of Variance (ANOVA) and Kruskal-Wallis Tests

Parametric assumptions could not be verified for the mean species richness populations or mean water table depth populations, so the statistical design required nonparametric testing. In order to determine if any significant differences occurred between the treatment groups in terms of the mean water table depths and mean species richness's across both seasons, four Kruskal-Wallis tests were performed. The first two tested for differences in summer mean species richness and spring species richness between the treatment groups. The third tested for differences in summer mean water

table depths between the treatment groups. Lastly, the fourth tested for differences in spring mean water table depths between the treatment groups. The populations of mean percent sand passed all parametric assumptions; therefore, an ANOVA was run to test for differences in mean percent sand present between the treatment groups.

Factorial Analysis of Variance

A two factor, factorial analysis of variance with season and piezometer location as fixed factors was used to test for the effects of seasonality and piezometer location on mean species richness.

Simple Linear Regressions

Two simple linear regressions were used to test the relationships between the sampled continuous variables. The first regression tested if mean plant species richness was dependent on mean water table depth. This regression plotted the 16 mean water table depths by the 16 corresponding mean plant richness values (8 values of each variable for each season). The second linear regression tested if mean water table depth was dependent on mean soil texture (percent sand). This regression plotted the 16 mean water table depths by the 16 corresponding mean soil texture percentages.

CHAPTER III - RESULTS

Richness, Abundance, and Community Similarity

The summer data collection period yielded a total gamma diversity of 152 taxa. Of the taxa sampled, 25 species had a percent cover greater than or equal to 1% (Table A1). The five most dominant species were *Sarracenia alata*, *Ctenium aromaticum*, *Rhynchospora pusilla*, *Andropogon virginicus*, and *Rhynchospora chapmanii*, respectively. Percent cover collection in the spring resulted in a gamma diversity of 149 taxa. The 25 most abundant species for this sampling period also had a percent cover greater than 1% (Table A2). The five species with the highest percent cover in the spring were *Rhynchospora pusilla*, *Sarracenia alata*, *Andropogon virginicus*, *Ctenium aromaticum*, and *Eriocaulon compressum*, respectively. The 10 most abundant species for the wet treatment groups (Piezometers 3-7) differed from that of the 10 most abundant species from the drier treatment groups (Piezometers 1, 2, and 8). Sedges, grasses, and forbs [or “other herbs”] dominated the wet sites (Table A3), while the drier sites contained woodier shrub/tree species (Table A4). While woody species often encroach the wetter areas of the bog, they are naturally denser and more dominant in the dry/mesic regions.

The additional sampling of the quadrats over the sampling period of both seasons displayed a species accumulation curve that indicated Buttercup Flats is expressing high alpha and gamma diversity, but low beta diversity or low species overlap (Figure A1). The ANOSIM for the summer abundance data resulted in significant differences occurring between the treatment groups [$R= 0.662$, $P=0.0002$]; the ANOSIM for the spring abundance data also resulted in significant differences between treatment groups

[$R=0.682$, $P=0.0002$] (Figure A2). ANOSIM results indicate that each treatment group is unique in community composition. Replicate samples of plant species composition for both seasons did appear to separate into two distinct clusters along the gradient of axis 1 in NMDS ordination space (Figure A3). Furthermore, treatment groups 1, 2, and 8 also seem to slightly separate along the gradient of axis 2 (Figure A3).

Parametric Normality

The mean species richness data failed to meet the parametric assumptions due to unequal variances within the populations. Despite log and square root transformation efforts, rejection of the null hypothesis of the Bartlett's test was persistent. Thus, further analyses were conducted using two nonparametric Kruskal-Wallis tests. The mean water table depth populations for summer and spring also failed to meet parametric assumptions. Multiple rejections of the Shapiro-Wilk goodness of fit null hypotheses led to the selection of the nonparametric alternative, the Kruskal-Wallis test. The populations of mean percent sand in the soil successfully met all of the parametric assumptions. Failure to reject all eight Shapiro-Wilk goodness of fit null hypotheses indicated that all of the populations were not significantly different from normal ($W=0.799$, $P=0.09$; $W=0.987$, $P=0.94$; $W=0.959$, $P=0.77$; $W=0.905$, $P=0.45$; $W=0.953$, $P=0.73$; $W=0.842$, $P=0.20$; $W=0.975$, $P=0.87$; $W=0.962$, $P=0.79$). A Bartlett's test was used to test that the variances of the eight populations were equal. The results of the test ($F=0.8185$, $DF=7$, $P=0.5717$) led to the failure to reject the null hypothesis. Therefore, it was assumed that the variances of the populations were equal.

Effect of Seasonality and Piezometer Location

The two factor, factorial ANOVA yielded a significant interaction ($F_{7,240}=160.37$, $P=0.037$) between the two fixed factors. Therefore, it was concluded that the slopes of the eight piezometer locations were significantly different (Figure A4). Moreover, the effect of seasonality on mean species richness was significantly different between the eight treatment groups.

Species Richness Differences per Season

A Kruskal-Wallis test testing the mean species richness from Summer 2018 resulted in significant differences occurring between the piezometer locations ($\chi^2=35.64$, $DF=7$, $P<0.0001$). A nonparametric comparison post-hoc test (Wilcoxon each-pair method) determined Piezometer 8 ($\mu=23.7$ sp.) was significantly more diverse than Piezometers 3-6. Piezometer 8 was not significantly more diverse than Piezometers 2 ($\mu=20.1$ sp.) and 7 ($\mu=21.1$ sp.) (Figure A5). The Kruskal-Wallis test for the mean species richness from Spring 2019 resulted in significant differences occurring between the piezometer locations, as well ($\chi^2=62.35$, $DF=7$, $P<0.0001$). Similar to the Summer 2018 data, a nonparametric comparison post-hoc test (Wilcoxon each-pair method) yielded that Piezometer 8 ($\mu=22.4$ sp.) was significantly more diverse than Piezometers 2-6 but was not significantly more diverse than Piezometer 7 ($\mu=21.5$) (Figure A5).

Water Table Depth Differences per Season

The Kruskal-Wallis test testing the mean water table depths from Summer 2018 resulted in significant differences occurring between the treatment groups ($\chi^2=119.98$, $DF=7$, $P<0.0001$). A nonparametric comparison post-hoc test (Wilcoxon Method) determined Piezometer 2 ($\mu=2.19$ m) was significantly drier than the other treatment

groups; Piezometer 8 was significantly drier than Piezometer 1. Piezometers 8 ($\mu = 1.81$ m) and 1 ($\mu = 1.17$ m) were also significantly drier than Piezometers 3-7 (Figure A6). The Kruskal-Wallis test testing the mean water table depths from Spring 2019 resulted in significant differences occurring between the treatment groups as well ($\chi^2 = 120.89$, $DF = 7$, $P < 0.0001$). Again, a nonparametric comparison post-hoc test (Wilcoxon Method) determined Piezometer 2 ($\mu = 1.20$ m) was significantly drier than the other treatment groups; Piezometer 8 was significantly drier than Piezometer 1. Similarly, Piezometer 8 ($\mu = 0.97$ m) and Piezometer 1 ($\mu = 0.34$) had significantly lower water tables than Piezometers 3-7 (Figure A6).

Soil Texture Differences

There were significant differences between the treatment groups in terms of mean percentage of sand in the soil ($F_{7, 24} = 28.25$, $P < 0.0001$). A Tukey's HSD post-hoc yielded that Piezometer 2 ($\mu = 0.11$) had significantly more sand in the soil than Piezometer 1 and Piezometers 3-8. Piezometers 7 and 8 did not have significantly more sand than Piezometers 1 and 5, but Piezometers 7 and 8 did have significantly higher levels of sand than Piezometers 3, 4, and 6 (Figure A7).

Soil Carbon

It was determined from the ANOVA that there were significant differences in percent inorganic carbon between the treatment groups $F_{7, 31} = 7.1981$, $P < 0.0001$. A Tukey's HSD post-hoc yielded Piezometer 1 ($\mu = 1.12\%$) contained significantly more inorganic carbon than Piezometers 3-7, yet not significantly more than Piezometer 2 ($\mu = 0.87\%$) and Piezometer 8 ($\mu = 0.82\%$).

Soil Nitrogen

The ANOVA determined significant differences in percent nitrogen occurred between the treatment groups ($F_{7,31} = 4.9076$, $P < 0.0015$). The Tukey's HSD post-hoc test yielded Piezometer 1 ($\mu = 0.0675$) had significantly more percent nitrogen than all other treatment groups, which were not significantly different from one another.

Soil Phosphorus

Significant differences between the treatment groups in terms of mean percent phosphorus ($F_{7,31} = 8.7970$, $P < 0.0001$) were obtained. The Tukey's HSD post-hoc test yielded Piezometer 1 ($\mu = 0.00375$) had significantly more phosphorus than all the other treatment groups except Piezometer 2 ($\mu = 0.00300$). Piezometer 2 was not significantly different than Piezometer 3 ($\mu = 0.00175$) and Piezometer 6 ($\mu = 0.00175$).

Dependency of Environmental Factors

The test of the dependency of species richness on water table depth using a simple linear regression was not significant ($F_{1,14} = 2.57$, $P = 0.131$). It was therefore concluded that mean species richness was not significantly dependent on mean water table depth (Figure A8a). The simple linear regression used to test if water table depth was dependent on soil texture resulted in a significant dependence ($F_{1,14} = 12.89$, $P = 0.003$) (Figure A8b). Therefore, it was concluded that mean percentage of sand in the soil had a significant, positive effect on mean water table

CHAPTER IV – DISCUSSION

Plant diversity during the summer at Buttercup Flats was slightly greater than spring diversity (152 vs. 149 taxa, respectively). Species accumulation over both seasons show curves that rise rapidly as common species are sampled, then the lines plateau as rarer species are identified (Figure A1). The nature of the curves indicate that Buttercup Flats is expressing high α and γ diversity, but low β diversity among the treatment groups. Kaeser and Kirkman (2009) claim non-parametric estimates such as species accumulation curves may not be the most accurate method to estimate species richness. For the purposes of this study, the accumulation patterns will serve as supplementary estimators of α , β , and γ diversity.

Species dominance between spring and summer collection periods were also very similar. The two collections yielded high dominance of graminoid and herbaceous species overall (Table A1 and Table A2); *Sarracenia alata* was the most dominant forb and the most dominant species collected overall during Summer 2018. This finding is not surprising, as *Sarracenia alata* has been noted as a well-distributed perennial herb in the western Gulf Coastal Plain, though its distribution is rather disjunct overall (Carstens and Satler 2013). The graminoid dominance over both sampling periods was primarily by the genera *Rhynchospora*, *Andropogon*, and *Ctenium*, as well as several other genera in the order *Poales*. The spring collection did show increased dominance of native holly species, *Ilex coriacea* and *Ilex vomitoria*, indicating the cyclic regime of prescribed fire was due for this landscape. Disruption of fire regimes allows woody species to encroach into savanna bog habitat (Martin and Smith 1991; Drewa et al. 2002). Overall, wet treatment groups displayed a very different species abundance than the dry treatments.

Wet plots exhibited high dominance of sedges (*Rhynchospora*) and a plethora of herbaceous species (Table A3), while dry treatments displayed elevated dominance of woody species (Table A4). Discrepancies in species dominance between wet and dry plots is an indicator that soil moisture is contributing to species composition at each site.

With species dominance changing across the environmental gradient, the goal of the next objective was to determine if species composition was similar across the study transect. The analyses of similarity of both seasons of herbaceous data yielded significant R values indicating that each treatment group was significantly dissimilar from each other in terms of species composition (Figure A2). Ordination of Summer 2018 data (Figure A3a) displayed that the dry treatment groups (Piezometers 1, 2, 8) formed a distinct cluster apart from the other treatment groups along Axis 1; furthermore, the dry treatment groups dispersed from each other vertically along Axis 2. The same pattern occurred along Axis 1 of the Spring 2019 ordination (Figure A3b). The clear separation of the two clusters along Axis 1 of both ordinations provides sufficient evidence that there is an observable environmental gradient contributing to species composition at each treatment group.

The fixed factors of seasonality and piezometer location (treatment group) were determined to be significantly interacting to affect mean species richness (Figure A4). Seasonal effects on mean species richness were significantly different between the piezometer locations. Mean species richness was significantly greater at each piezometer location during the summer collection period; Piezometer 8 was significantly more diverse than any other treatment group across both sampling seasons. Piezometer 8 also had the second highest (driest) mean water table depth. Piezometer 2 was the driest

treatment group even though it was lower in elevation than Piezometer 1. Furthermore, Piezometers 1, 2, and 8 had the highest percentages of sand in the soil, though Piezometer 2 had significantly more sand in the soil than any other treatment group.

It was determined via regression that mean species richness was not dependent on the mean water table depth, meaning the observed patterns of diversity across the transect were not intrinsically linked to water table depth (Figure A8a). However, ordination patterns from more upland (and thus drier and sandier) piezometer locations (1, 2, 8) clustered together along the left side of Axis 1 (Figure A3), therefore providing evidence that soil moisture could be a gradient driving plant species composition. Regression also revealed the mean water table depths were significantly dependent on soil texture or percent sand in the soil (Figure 8b). The percentage of sand in the soil profile may explain why Piezometer 1 had shallower water table depths at a higher elevation than Piezometer 2, which had over three percent more sand than Piezometer 1. Solbrig (1993) observed localized herbaceous communities in savanna habitats and postulated that patterns in community structure tend to be strongly associated with geomorphological characteristics. It is proposed that soil texture (percent sand) may have influenced plant community structure along with soil moisture or other potential environmental factors.

Elevational gradients shaped by variations in topography are formed from substantial weathering processes as exhibited by the highly weathered soils of the Gulf Coastal Plain (Drewa et al. 2002). Moreover, elevation gradients regulate observable differences in soil moisture levels occurring along the undulating topography of pine savanna ecosystems (Drewa et al. 2002). In agreement with Drewa et al. (2002), Piezometers 2, 8, and 1, respectively, are the significantly driest treatment groups, as well

as the treatment groups occurring at the highest elevations. It should be noted, however, that quantitative measures of elevation were not recorded in this experimental design. Nevertheless, this study provides evidence that elevation may be a key abiotic factor contributing to soil texture which drives differences in soil moisture and plant community structure, perhaps even contributing to plant richness levels at each treatment group.

In terms of species richness, Piezometer 8 was repeatedly the most significantly diverse treatment group (Figure A5). The plots established at Piezometer 8 displayed richness qualities typically found in well-managed, mesic pine savanna habitats. It is proposed that mesic pine savanna ecosystems exhibit higher plant diversity levels than the wet, boggy savanna ecosystems as observed at Buttercup Flats in De Soto National Forest. The wetter sites were quite diverse, but richness seemed to be increasingly limited as surface soil moisture increased. Mesic pine regions neighboring wetland pine savannas accumulate broader ranges of plant species from upland pinelands and seepage bogs. Drewa et al. (2002) states that many woody species may be less sensitive to changes in edaphic factors, such soil texture and moisture. Tree/shrub species distributions are more expansive and dynamic than herb species distributions, making it possible for woody species to encroach wet pine savannas (Bourliere and Hadley 1983). Adequate management via prescribed fire is the primary practice used in southern Mississippi for reducing woody species densities and promoting herbaceous growth (Platt et al. 1988; Glitzenstein et al. 1995).

There are three areas of research that could branch off this study that would improve our current understanding of the effects of abiotic, edaphic factors on plant species richness and community composition. (1) The continuation of the current

experimental design over several years of observation and increased sampling. Observing the patterns of water table depths and richness levels long term will provide further clarity of ecological relationships. (2) The addition of elevation as a factor in the experimental design would provide increased insight to the ecological factors driving plant community structure. Furthermore, quantitative observations of an elevation gradient would increase our understanding of the impact elevation has on edaphic factors, such as water table depth, surface soil moisture, and soil texture. (3) Repetition of the current experimental design after a prescribed burning treatment to test for the effects of fire on plant diversity and water table depth. The removal of woody species from the study sites would improve the precision of the herbaceous cover data thereby increasing the accuracy of the statistical analyses.

APPENDIX– Tables and Figures

Table A1. August 2018 Top 25 Species (Percent Cover)

| Species | Total Percent Cover | Habit |
|---------------------------------|---------------------|----------|
| <i>Sarracenia alata</i> | 16.96 | Forb |
| <i>Ctenium aromaticum</i> | 15.63 | Grass |
| <i>Rhynchospora pusilla</i> | 14.35 | Sedge |
| <i>Andropogon virginicus</i> | 12.21 | Grass |
| <i>Rhynchospora chapmanii</i> | 10.88 | Sedge |
| <i>Schizachyrium tenerum</i> | 9.39 | Grass |
| <i>Rhynchospora gracilentia</i> | 8.63 | Sedge |
| <i>Eriocaulon decangulare</i> | 6.46 | Forb |
| <i>Ilex coriacea</i> | 5.32 | Shrub |
| <i>Balduina uniflora</i> | 4.51 | Forb |
| <i>Xyris iridiolia</i> | 4.27 | Forb |
| <i>Muhlenbergia expansa</i> | 3.91 | Grass |
| <i>Ilex glabra</i> | 3.81 | Shrub |
| <i>Zigadenus glaberrimus</i> | 3.41 | Forb |
| <i>Helianthus heterophyllus</i> | 2.74 | Forb |
| <i>Aristida palustris</i> | 2.69 | Grass |
| <i>Eriocaulon compressum</i> | 2.69 | Forb |
| <i>Dichanthelium ensifolium</i> | 2.39 | Grass |
| <i>Pityopsis graminifolia</i> | 2.39 | Forb |
| <i>Nyssa sylvatica</i> | 2.37 | Tree |
| <i>Ilex vomitoria</i> | 2.31 | Shrub |
| <i>Aristida purpuracens</i> | 2.2 | Grass |
| <i>Gaylussacia dumosa</i> | 2.16 | Subshrub |

Table A1 (continued).

| | | |
|---------------------------------|------|-------|
| <i>Carex bullata</i> | 2.07 | Sedge |
| <i>Dichanthelium acuminatum</i> | 2.0 | Grass |

Table A1

The 25 most abundant plant species from Buttercup Flats in De Soto National Forest (MS), collected August 2018. Total percent cover incorporates zero values in the calculation; $n=128$ for the sampled quadrats. Most of the species were grass, sedge, and forb species.

Table A2. April 2019 Top 25 Species (Percent Cover)

| Species | Mean Percent Cover | Habit |
|---------------------------------|--------------------|----------|
| <i>Rhynchospora pusilla</i> | 14.11 | Sedge |
| <i>Sarracenia alata</i> | 11.9 | Forb |
| <i>Andropogon virginicus</i> | 9.45 | Grass |
| <i>Ctenium aromaticum</i> | 9.31 | Grass |
| <i>Eriocaulon compressum</i> | 7.82 | Forb |
| <i>Ilex coriacea</i> | 5.98 | Shrub |
| <i>Rhynchospora plumosa</i> | 5.44 | Sedge |
| <i>Gaylussacia dumosa</i> | 5.12 | Subshrub |
| <i>Schizachyrium tenerum</i> | 4.71 | Grass |
| <i>Eriocaulon decangulare</i> | 4.6 | Forb |
| <i>Muhlenbergia expansa</i> | 4.11 | Grass |
| <i>Ilex vomitoria</i> | 3.52 | Shrub |
| <i>Dichanthelium tenue</i> | 3.48 | Grass |
| <i>Nyssa sylvatica</i> | 3.18 | Tree |
| <i>Drosera capillaris</i> | 3.15 | Forb |
| <i>Helianthus heterophyllus</i> | 3.09 | Forb |
| <i>Ilex glabra</i> | 2.91 | Shrub |
| <i>Balduina uniflora</i> | 2.79 | Forb |
| <i>Carex bullata</i> | 2.59 | Sedge |
| <i>Lophiola aurea</i> | 2.1 | Forb |
| <i>Rhexia alifanus</i> | 1.71 | Forb |
| <i>Andropogon mohrii</i> | 1.59 | Grass |
| <i>Gaylussacia mosieri</i> | 1.46 | Subshrub |
| <i>Aristida purpurascens</i> | 1.42 | Grass |

Table A2 (continued).

| | | |
|--------------------------------|------|----------|
| <i>Hypericum brachyphyllum</i> | 1.37 | Subshrub |
|--------------------------------|------|----------|

Table A2

The 25 most abundant species in terms of percent cover from Buttercup Flats in De Soto National Forest (MS), collected April 2019.

All zeroes for total percent cover were incorporated in the calculation; $n=128$ for sampled quadrats. Most of the species were grasses, sedges, and forbs, but there was an increase in the abundance of woody shrubs in the spring.

Table A3. *Wet Treatment Group's Top 10 Species (Percent Cover)*

| Species | Mean Percent Cover | Habit |
|---------------------------------|--------------------|-------|
| <i>Sarracenia alata</i> | 15.36 | Forb |
| <i>Ctenium aromaticum</i> | 13.63 | Grass |
| <i>Rhynchospora pusilla</i> | 13.03 | Sedge |
| <i>Rhynchospora plumosa</i> | 10.72 | Sedge |
| <i>Rhynchospora gracilentia</i> | 8.27 | Sedge |
| <i>Eriocaulon decangulare</i> | 6.1 | Forb |
| <i>Balduina uniflora</i> | 4.26 | Forb |
| <i>Xyris laxifolia.</i> | 4.02 | Forb |
| <i>Eriocaulon compressum</i> | 2.69 | Forb |
| <i>Zigadenus.glaberrimus</i> | 2.54 | Forb |

Table A3:

The 10 most abundant species from the wet treatment groups (Piezometers 3-7) at Buttercup Flats in De Soto National Forest. All zeroes for total percent cover were incorporated in the calculation; $n=80$ for sampled quadrats. Herbs and sedges dominated species abundance with the notable absence of woody species.

Table A4. *Dry Treatment Group's Top 10 Species (Percent Cover)*

| Species | Mean Percent Cover | Habit |
|-------------------------------|--------------------|----------|
| <i>Andropogon virginicus</i> | 10.08 | Grass |
| <i>Schizachyrium tenerum</i> | 8.22 | Grass |
| <i>Ilex coriacea</i> | 4.61 | Shrub |
| <i>Ilex glabra</i> | 3.31 | Shrub |
| <i>Muhlenbergia expansa</i> | 2.6 | Grass |
| <i>Pityopsis graminifolia</i> | 2.36 | Forb |
| <i>Ilex vomitoria</i> | 2.31 | Shrub |
| <i>Gaylussacia dumosa</i> | 2.15 | Subshrub |
| <i>Aristida purpurascens</i> | 2.08 | Grass |
| <i>Pityopsis adenolepis</i> | 1.82 | Forb |

Table A4:

The 10 most abundant species from the dry treatment groups at Buttercup Flats in De Soto National Forest. Total percent cover incorporates zero values in the calculation; $n=48$ for the sampled quadrats. Dry treatment groups were dominated by holly species and common pine savannah grasses.

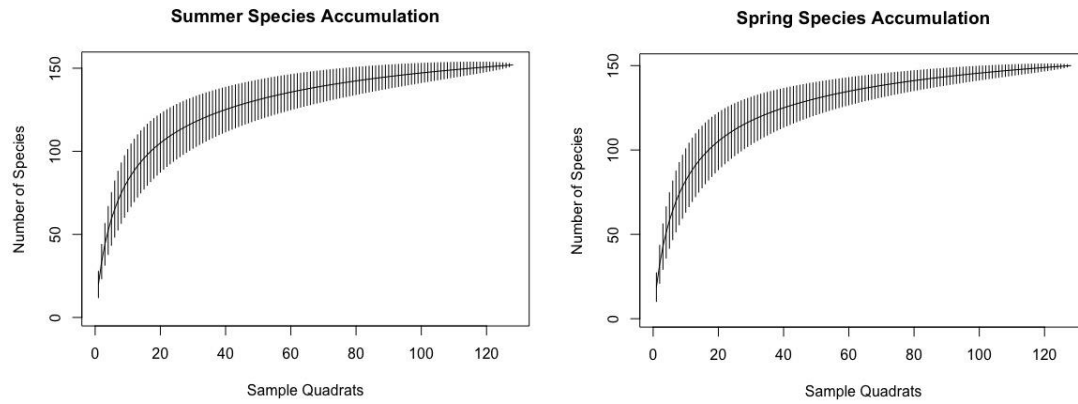


Figure A1. *Species Accumulation Curves*

Species accumulation curves displaying the rate of new species being recorded with additional sampling of the quadrats. The curve rises quickly at first as common species are sampled then plateaus as rarer species are discovered. The nature of the curve indicates Buttercup Flats is expressing high alpha and gamma diversity, but low beta diversity.

| Season | ANOSIM R | <i>P</i> -value |
|-------------|----------|-----------------|
| Summer 2018 | 0.662 | 0.0002 |
| Spring 2019 | 0.682 | 0.0002 |

Figure A2. *Analyses of Similarity*

ANOSIM R values and significance levels for plant species composition (in terms of abundance). ANOSIM used 5000 permutations.

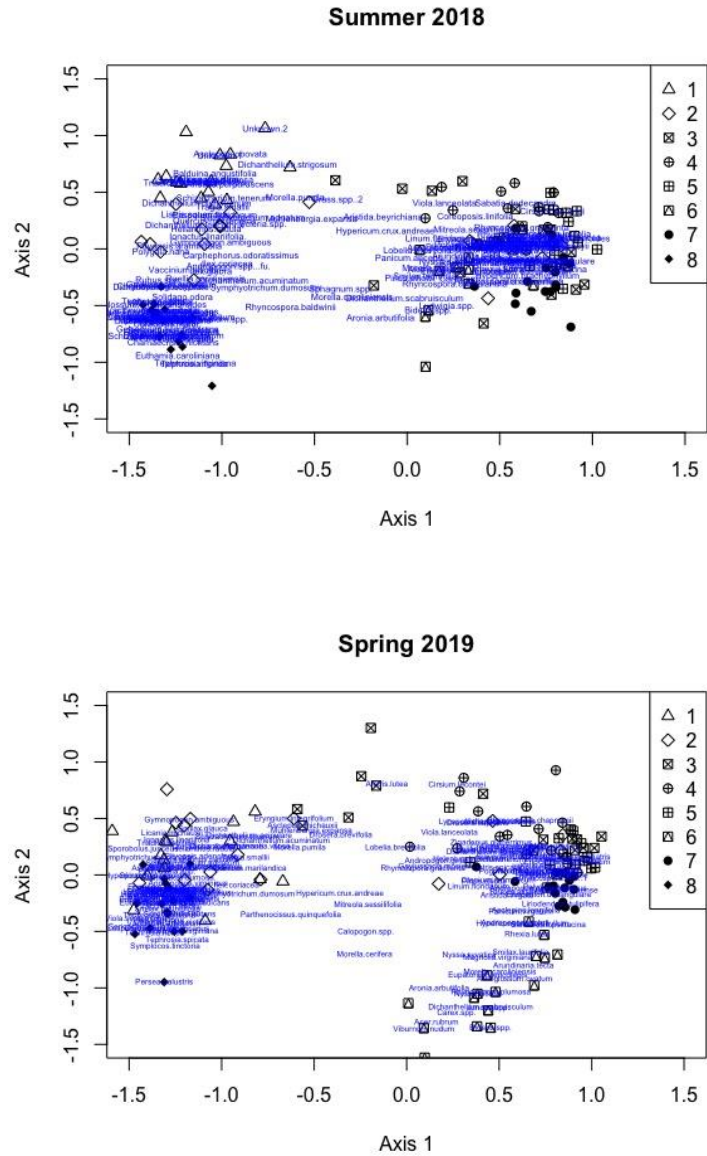


Figure A3. NMDS Ordinations for Summer 2018 and Spring 2019

NMDS ordinations of the percent cover abundance for Summer 2018 and Spring 2019. Clear separation and clustering can be seen along Axis 1 of both ordinations. Separation between Piezometer 1, 2, and 8 along Axis 2 is apparent (Fig A3a), while separation of Piezometer 6 is clear along Axis 2 of the Spring ordination (Fig A3b).

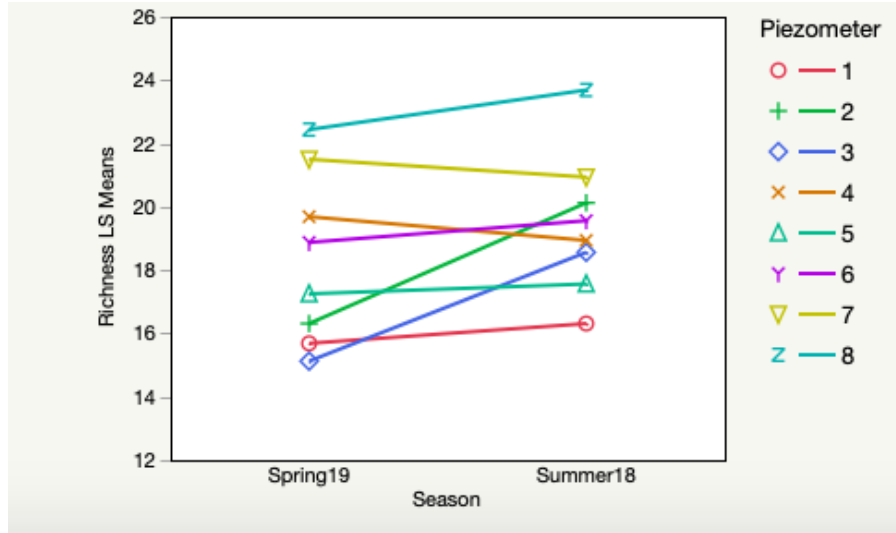


Figure A4. *Two Factor, Factorial ANOVA Interaction Plot*

Two factor, factorial ANOVA interaction plot showing the significant interaction of seasonality and piezometer location factors. The plotted lines are displaying the slopes of the lines are not equivalent; therefore, the seasonality is significantly affecting mean species richness at each piezometer location.

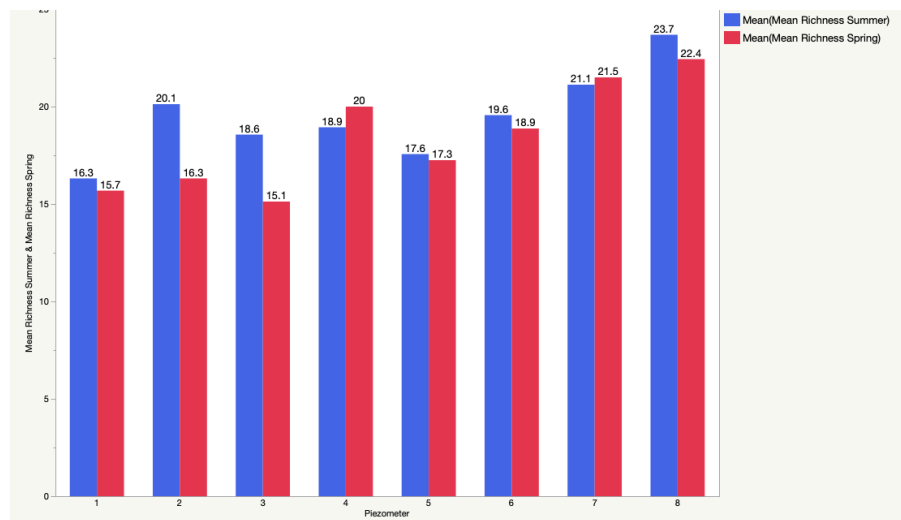


Figure A5. *Mean Species Richness for Each Treatment Group*

Mean species richness for each treatment group at Buttercup Flats across both seasons of collection. Piezometer 8 had the highest average overall over both seasons; n-16 for each treatment group. (Summer=blue; Spring=red).

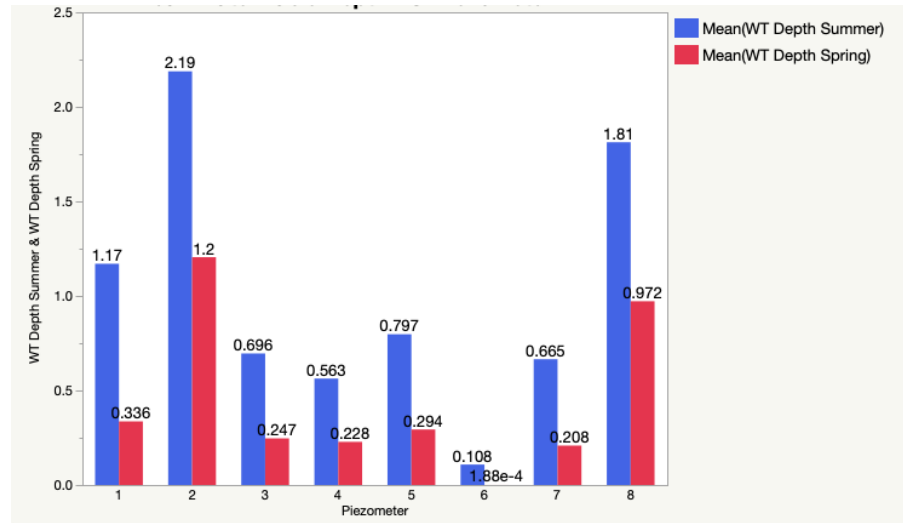


Figure A6. *Mean Water Table Depth for Each Treatment Group*

Mean water table depth for each treatment group at Buttercup Flats across both seasons of collection. Piezometer 2 ($\mu = 2.19$ m) had the highest water table depth followed by Piezometers 8 ($\mu = 1.81$ m) and 1 ($\mu = 1.17$ m), respectively, over both sampling seasons. Mean depths were calculated using a 60-day average of sensor depths. (Summer=blue; Spring=red).

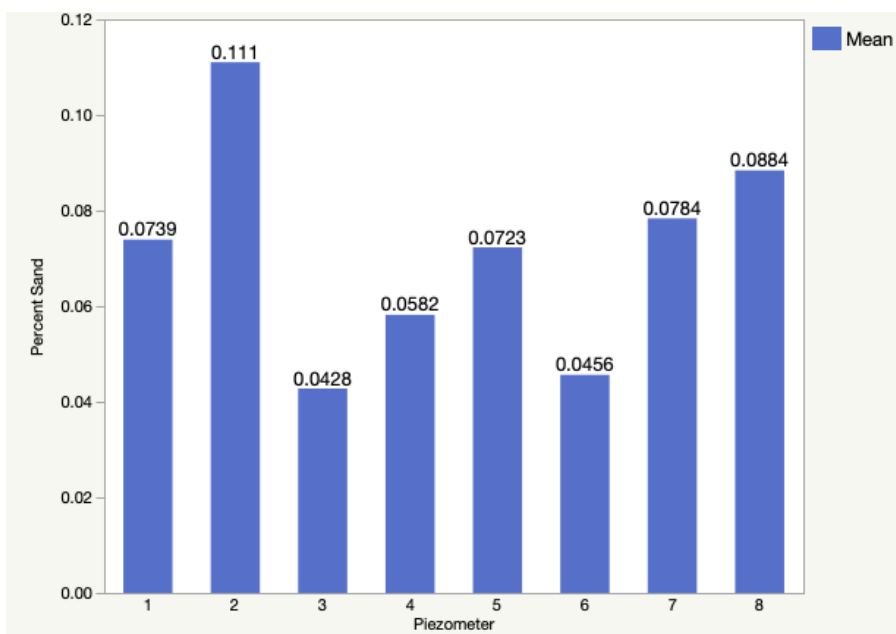


Figure A7. *Mean Percent Sand in the Soil for Each Treatment Group*

Mean percent sand in the soil for each treatment group at Buttercup Flats in De Soto National Forest (n=32). Piezometer 2 ($\mu=0.11$) had significantly more sand in the soil than any other treatment group ($P<0.0001$).

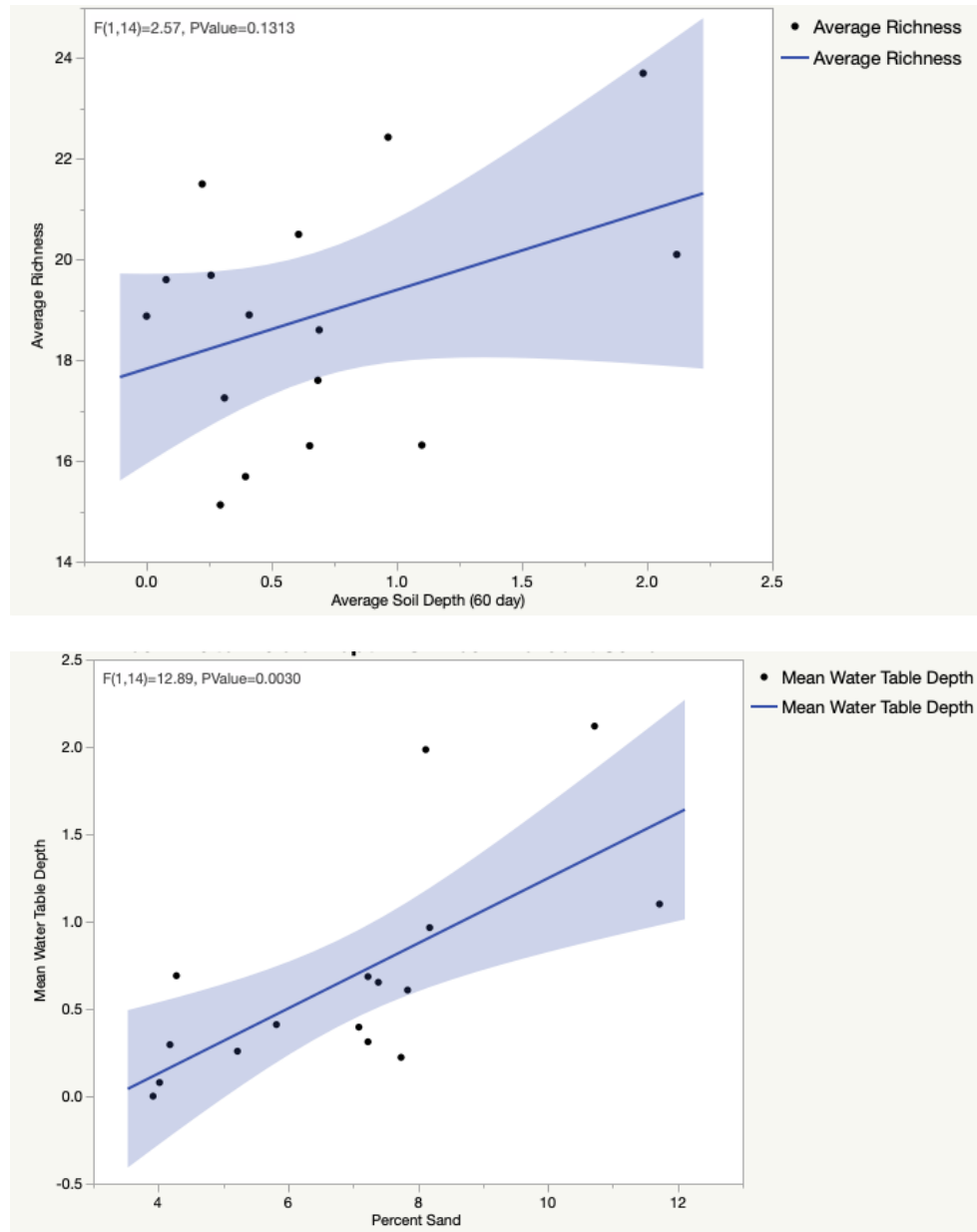


Figure A8. *Simple Linear Regressions of Edaphic Characteristics*

Simple linear regression (top) shows that mean species richness is not dependent on water table depth due to an insignificant line of fit ($P=0.1313$); $n=16$ for mean richness values and mean water table depths. Simple linear regression (bottom) displaying mean water table depth is significantly dependent on percent sand in the soil ($P=0.003$).

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